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DETECTION OF PASSERINES' LOOP MIGRATION PATTERN USING WING LENGTH MEASUREMENTS

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Bird species following a loop migration strategy use different routes during autumn than in the spring season. Birds nesting at different latitudes have different wing morphology. Finding significant differences in the average wing lengths of the same species between the autumn and spring seasons in the same area suggests loop migration. If these differences are also different by sex, this suggests that males and females do not use the same migratory routes. In this study, we analysed wing morphological differences of seven common long-distance migrant passerine species ringed at the Ócsa Bird Ringing Station from 1984 to 2014. Species were divided into three groups based on moult strategies (pre-, postnuptial and double moult). Based on differences in wing length distributions and means between autumn and spring, six of the seven passerine species follow loop migration. While wing length differences can be adequate to detect loop migration, the species specific moult strategies, the nesting sites and distribution ranges need to be known.

Keywords: loop migration, wing length distribution, prenuptial and postnuptial moult.

INTRODUCTION

Loop or elliptical migration is a widespread migration pattern which occurs in different taxa (e.g. McKinnon *et al.* 2013). Birds following loop migration do not use the same route in the spring and autumn seasons (e.g. Alerstam 1990, Berthold 2001, Newton 2008). They can move in a westerly or easterly direction on their return journey, performing a clockwise loop, such as the European Nightjar *(Caprimulgus europaeus)* (Jacobsen *et al.* 2017, Norevik *et al.* 2017), or the Common Cuckoo *(Cuculus canorus)* (Willemoes *et al.* 2014, Jacobsen *et al.* 2017). A counter-clockwise loop migration is performed by the Reed Warbler *(Acrocephalus scirpaceus)* (Procházka *et al.* 2016) and Red-backed Shrike *(Lanius collurio)* (Zink 1975, Berthold 2001, Tøttrup *et al.* 2012). The size and shape of the loop may differ between populations and even between sexes of the same species (Newton 2008, Harnos *et al.* 2015*a*,*b*).

Wing morphology can also be different among different populations of the same species. Birds which migrate over longer distances have on average longer and more pointed wings because they are strongly influenced by

selective pressure (faster and/or energy-efficient flight) (Norberg 1995). Birds originating from southern regions and migrating shorter distances to their wintering grounds have shorter and more rounded wings (Holynski 1965, Tiainen & Hanski 1985, Marchetti *et al.* 1995, Lockwood *et al.* 1998, García-Peiró 2003). This pattern allows to distinguish between the different populations, at least statistically (e.g. Lövei 1979, 1983, Lockwood *et al.* 1998, Perez-Tris & Telleria 2001, García-Peiró 2003). If the wing length distribution of adult migrant birds differs between spring and autumn in the same area, it is possibly due to a change in the composition of the migrants with different origins, indicating a possible loop migration pattern (Ożarowska *et al.* 2011, Jónás *et al.* 2012, 2015).

Getting an insight into the moult strategies of a species is indispensable for interpreting these differences. Some species moult during summer, between the end of the nesting season and the autumn migration (postnuptial moult). Others replace their old feathers with new ones during winter, before starting the return migration in spring (prenuptial moult); other species moult in both seasons (double moult) (Ginn & Melville 1983, Svensson 1992, Jenni & Winkler 1994). The moult in all cases leads to an increase in wing length. This increase is different among species but in small passerines, it is not more than a few tenths of a millimeter (in average 0.4–0.8 mm) (Norman 1997). The greatest growth of the wing length occurs during the first moult. This change decreases with age, but even then it is detectable in case of some species (e.g. Stewart 1963, Norman 1983, Alatalo *et al.* 1984, Hogstad 1985).

If individuals of a species performing postnuptial moult have shorter average wing length in autumn than in spring in an area, one can suspect that these individuals do not belong to the same population, and the species probably performs loop migration. If birds with postnuptial moult have longer wings on average in autumn than in spring, but the degree of increase exceeds the expected growth from the moult, elliptical migration can also be suspected. The inverse case is an evidence of loop migration for species with prenuptial moult. If these birds have shorter average wing length in spring than in autumn at the same study area, the composition of the trans-migrant population is almost certainly different in the two seasons. If individuals of species doing prenuptial moult have longer wings on average in spring than in autumn, but the degree of the increase exceeds the expected growth from the moult, the outward and return migration routes are probably different.

The main goal of our study was to examine if there are such differences present in trans-migrant populations of passerine bird species at the Ócsa Bird Ringing Station between spring and autumn (representing populations migrating through the Carpathian Basin). Therefore, we investigated the following questions:

Are the average wing lengths and wing length distributions of captured birds different between spring and autumn, taking into account the moult strategy of the given species?

Is there a difference in the pattern of loop migration between sexes in case of species showing sexual dimorphism?

MATERIAL AND METHODS

We analysed the database of the Ócsa Bird Ringing Station (47°15'N, 19°15'E) collected between 1984 and 2014. The station is located on the northern part of the Ócsa Landscape Protection Area (called Öregturján peatland), in the Duna-Ipoly National Park in Hungary. Large part of this area is internationally protected by the Natura 2000 network and the Ramsar Convention on wetlands.

We analysed wing length data of individuals from the following seven common long-distance migrant species (approximately 4700 individuals): Common Nightingale *(Luscinia megarhynchos)*, Savi's Warbler *(Locustella luscinioides)*, Wood Warbler *(Phylloscopus sibilatrix)*, Willow Warbler *(Phylloscopus trochilus)*, Spotted Flycatcher *(Muscicapa striata)*, Pied Flycatcher *(Ficedula hypoleuca)*, Red-backed Shrike *(Lanius collurio)*. Birds were captured with mist nets in diverse habitats, with standard methods, following the methods of the Actio Hungarica (AH) bird ringing network (Szentendrey *et al.* 1979). Individuals were identified to species, age and sex (if it was possible), and were ringed with individually numbered, appropriate-sized aluminium rings. From the recorded biometric data (Szentendrey *et al.* 1979), only the wing length and the degree of the abrasion of the primary feathers were used.

The degree of the abrasion of the primaries was scored on a scale of 0-3 (0: intact, 1: minimally worn, 2: worn, but measurable, 3: heavily worn, cannot be measured). In our study, only birds with intact or minimally worn primaries were included. Wing length, was measured by the 'maximum flattened chord method' (Svensson 1992) to the nearest 1 mm. To take into account the variability in measurements caused by different bird ringers, we included the ringer as a random factor in the applied general linear mixed model (GLMM).

For the analysis only the wing length data of adult birds was used because of the considerable wing length growth during the first moult in juvenile birds (Stewart 1963, Alatalo *et al.* 1984).

The adult individuals from three of the seven species – the Common Nightingale, Savi's Warbler and the Pied Flycatcher – do postnuptial moult. Adult birds of one species – Willow Warbler – moult in both seasons. The adults of the other three species – Wood Warbler, Spotted Flycatcher and Red-backed Shrike – perform prenuptial moult (Svensson 1992).

We compared average autumn and spring wing length values using Welch's t-test (Reiczigel *et al.* 2014). For the two species showing sexual dimorphism, Pied Flycatcher and Red-backed Shrike, sexes were analysed separately. The defined spring migration period lasts until the 151st day of the year (31 May), and the autumn migration period starts on 1 August (based on capture – recapture frequencies). The statistical analysis was done in R 3.2.2 (R Core Team 2015) using the "*nlme*" package to fit GLMM models (Pinheiro *et al.* 2017). Smoothed histograms serve the goal to show the distribution curves.

RESULTS

Species performing postnuptial moult

The average wing length of two species (Common Nightingale, Savi's Warbler) out of those performing postnuptial moult was significantly shorter in autumn than in the spring. The average wing length differences were significant (–0.9 mm and –1.9 mm). Pied Flycatchers had longer wing on average (0.6 mm) in autumn than in spring (Table 1).

The spring and autumn wing length smoothed histograms of the Common Nightingale showed overlap (Fig. 1*A*), but in autumn the proportion of shorter winged birds was greater. The shape of the curves of the Savi's Warbler was similar, partially overlapped with a significant difference between spring and autumn, and the proportion of shorter winged birds was greater than expected from a normal distribution (Fig. 1*B*). The shape of the curves of the Pied Flycatcher were also similar (Figs 1*C* and 1*D*).

Table 1. Average (±SD) spring and autumn wing length data of species performing postnuptial moult and differences with p-values.

	Sample size		Wing length mean±SD (mm)		Difference (mm)	p-value
	spring	autumn	spring	autumn		
Common Nightingale	652	164	86.4±2.6	85.5±2.6	–0.9	<0.0001
Savi's Warbler	623	63	70.5±2.2	68.6±2.5	–1.9	<0.0001
Pied Flycatcher	425	325	80.2±2.0	80.8±2.3	0.6	0.0016

Table 2. Average (±SD) spring and autumn wing length data of male and female Pied Flycatcher with differences and p-values.

	Sample size		Wing length mean±SD (mm)		Difference (mm)	p-value
Within sexes						
	spring	autumn	spring	autumn		
Male	249	120	80.9±1.9	81.6±2.4	0.7	0.0028
Female	163	169	79.3±1.9	80.1±2.0	0.8	0.0002
Between sexes						
	male	female	male	female		
Spring	249	163	80.9±1.9	79.3±1.9	1.6	<0.0001
Autumn	120	169	81.6±2.4	80.1±2.0	1.5	<0.0001

Among the species showing sexual dimorphism and perform postnuptial moult, the average wing length of the Pied Flycatcher differed significantly between the two seasons, both in males and females. Both sexes had longer wings in autumn. Males also had significantly longer wings than females. The difference was significant in both seasons (Table 2).

Species performing prenuptial moult

The wings of species performing prenuptial moult were significantly longer in spring than in autumn, except for the Red-backed Shrike. The dif-

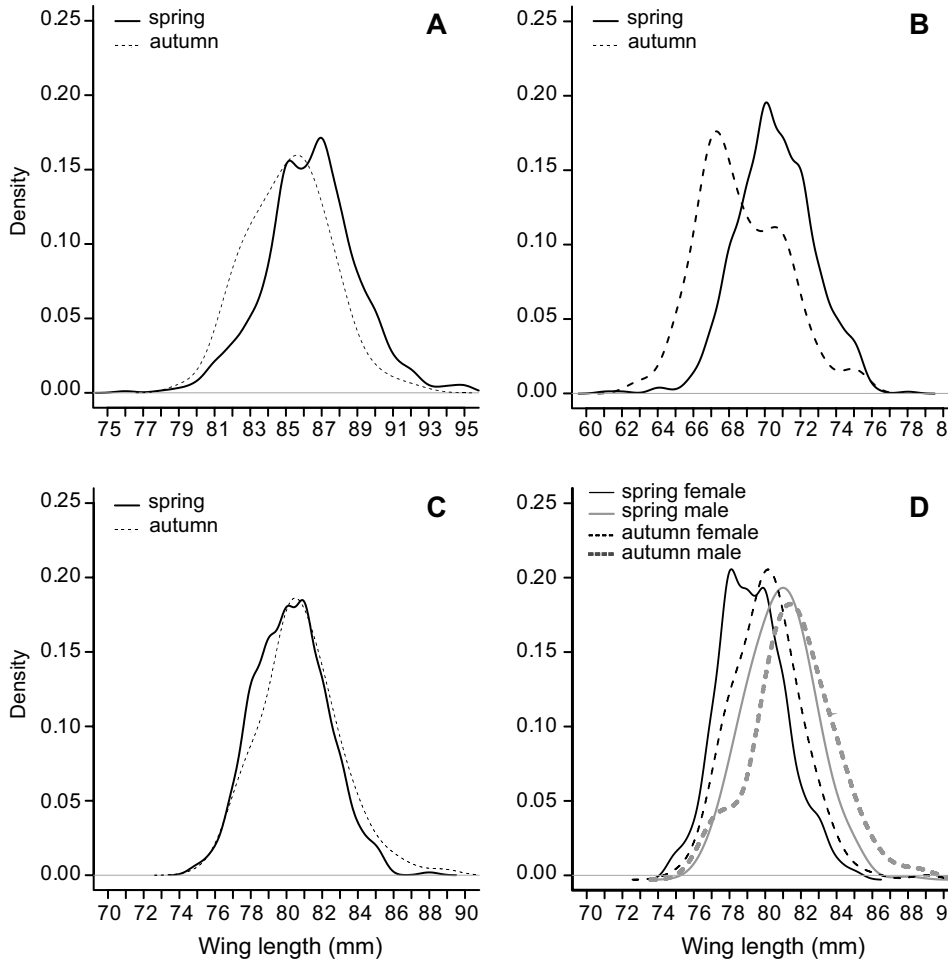

Fig. 1. Wing length distributions of species performing postnuptial moult. A = Common Nightingale, B = Savi's Warbler, C = Pied Flycatcher, D = Pied Flycatcher ♂♀

ferences in case of Wood Warbler and Spotted Flycatcher were 1.6 mm and 1.0 mm, respectively. The average wing length of Red-backed Shrikes did not differ significantly between seasons (Table 3).

Table 3. Average (±SD) autumn and spring wing length data of species performing prenuptial moult and differences with p-values.

	Sample size		Wing length mean±SD (mm)		Difference (mm)	p-value
	autumn	spring	autumn	spring		
Wood Warbler	441	386	75.3±2.5	76.9±2.2	1.6	<0.0001
Spotted Flycatcher	312	148	88.3±2.3	89.3±2.0	1.0	<0.0001
Red-backed Shrike	165	226	93.5±2.4	93.2±2.2	–0.3	0.1846

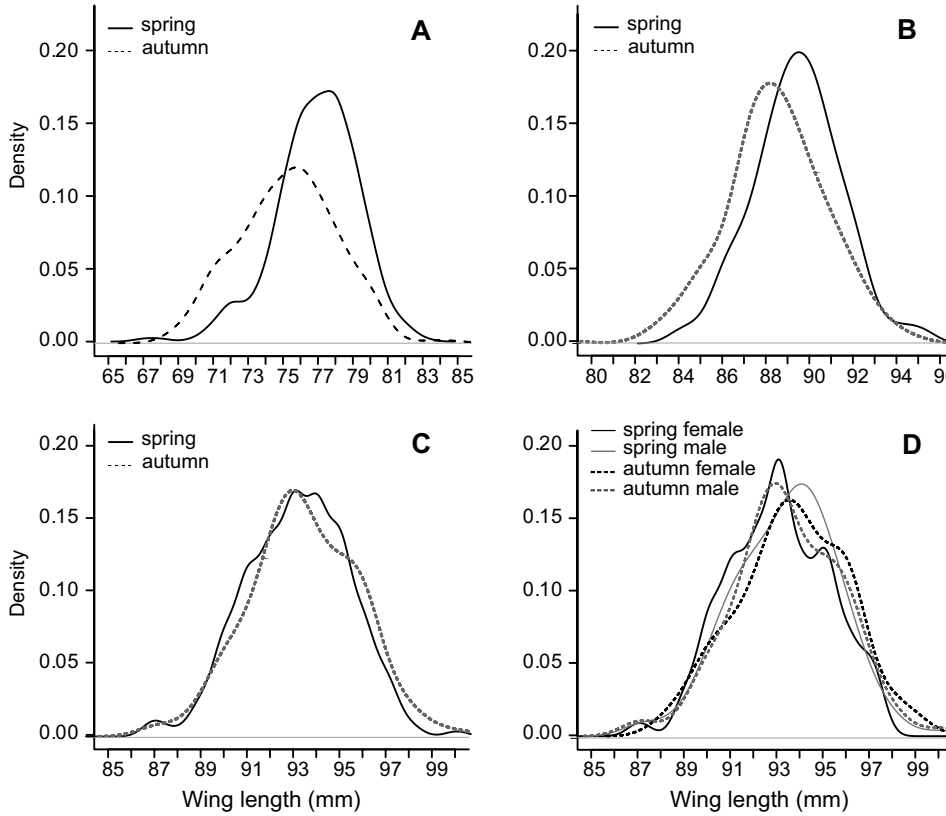

Fig. 2. Wing length distribution of species performing prenuptial moult. A = Wood Warbler, B = Spotted Flycatcher, C = Red-backed Shrike, D = Red-backed Shrike ♂♀

Table 4. Average (±SD) autumn and spring wing length data of male and female Red-backed Shrike with differences and p-values.

	Sample size		Wing length mean±SD (mm)		Difference (mm)	p-value
Within sexes						
	autumn	spring	autumn	spring		
Male	99	140	93.4±2.5	93.3±2.3	–0.1	0.6140
Female	66	86	93.6±2.4	93.0±2.2	–0.6	0.1072
Between sexes						
	male	female	male	female		
Spring	140	86	93.3±2.3	93.0±2.2	0.3	0.2734
Autumn	99	66	93.4±2.5	93.6±2.4	0.2	0.7627

Table 5. Average (±SD) spring and autumn wing length data of species performing double moult and difference with p-value.

	Sample size		Wing length mean±SD (mm)		Difference (mm)	p-value
	spring	autumn	spring	autumn		
Willow Warbler	190	380	68.5±2.55	66.7±2.82	–1.7	<0.0001

In the case of Wood Warbler (Fig. 2*A*) the shape of the autumn and spring wing length distribution curves was different, while in case of the Spotted Flycatcher (Fig. 2*B*) they were similar. The wing length distribution curves of the Red-backed Shrike were approximately the same (Figs 2*C* and 2*C*).

Among species performing prenuptial moult, the Red-backed Shrike shows sexual dimorphism in the color of plumage, but it was not apparent in wing length (Table 4, Figs 2*C*,*D*).

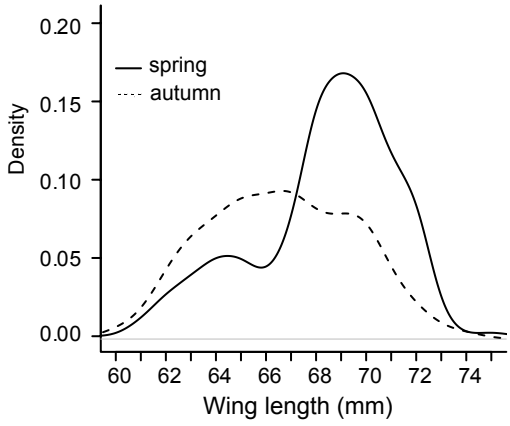

Fig. 3. Wing length distribution of species performing double moult Willow Warbler

Species performing double moult

The wing lengths of the Willow Warbler (performing double moult) differed significantly: the birds had much shorter (–1.7 mm, Table 5) wings in average in autumn than in spring. The shape of the wing length distribution curves were totally different (Fig. 3).

DISCUSSION

Capture-recapture data indicate the existence of a loop migration in some parts of Europe and Africa for the Wood Warbler, the Pied Flycatcher (Wernham *et al.* 2002), and the Red-backed Shrike (Zink 1975). In other species, the differences in the number of observed individuals in an area between spring and autumn suggests the existence of loop migration, such as for the Reed Warbler (Ożarowska *et al.* 2011, Zduniak *et al.* 2013), or the Blackcap *(Sylvia atricapilla)* (Zduniak *et al.* 2013). Unfortunately, most species have no or very few long-distance recapture data, and bird-survey data are often inaccurate. Using biometric data as an alternative method to detect loop migration can be promising. Capture-recapture data, once become available, can be used to confirm these results.

In our study, we detected differences in average wing lengths between spring and autumn in six of the analysed seven passerine species.

The Common Nightingale is a species migrating on a broad front. Populations originating from different breeding sites usually also have separate wintering areas in Africa. That is why it can be assumed that routes from the nesting areas to the wintering grounds are also different (Hahn *et al.* 2013). Although in regions north of the Carpathian Basin, many Common Nightingales are ringed, there is still no recapture demonstrating a migratory connection (Kováts & Csörgő 2009). We found a significantly longer wing length in spring than autumn despite the postnuptial moult, so Common Nightingales migrating through the Carpathian Basin probably belong to loop-migrating populations. In case of its sister species – the Thrush Nightingale *(Luscinia luscinia)* – the existence of loop migration pattern has already been detected by Kováts (2012).

The Savi's Warbler winters in the Sahel zone (Cramp & Brooks 1992). The Carpathian mountains appear as ecological barriers for birds breeding north of Hungary and probably only few of them migrate through this area. So far, four foreign-ringed birds were recaptured in Hungary during the autumn migration period (Gyurácz & Csörgő 2009*a*). In Europe, the average wing length of Savi's Warblers increases from west to east (Kulaszewicz *et al.* 2013). We found significantly longer wings in spring than autumn indicating loop migration. During the autumn period, wing length has small variance either in Poland (Kulaszewicz *et al.* 2013), or in Hungary (Mátrai *et al.* 2006). This fact suggests that trans-migrant birds originate from a restricted area. Within the distribution range of this species, sexual dimorphism in wing length was detected in several areas (males have longer wing than females) (Nowakowski 2002, Kulaszewicz *et al.* 2013), but this difference is not so large that possible differences between the migration of sexes could explain the differences found.

The Pied Flycatcher winters south of the Sahara, in the western African regions. Most of the individuals migrate through the Iberian Peninsula towards Africa, and fewer birds pass through the Italian Peninsula before reaching Africa (Cramp *et al.* 1993). A counter-clockwise loop migration is known in several populations. The direction of the autumn route is mainly through the Western Mediterranean region, while the spring route passes through the Central Mediterranean (Pilastro *et al.* 1998, Wernham *et al.* 2002, Bønløkke *et al.* 2006, Spina & Volponi 2008, Newton 2008, Török 2009*b*, Ouwehand *et al.* 2016). We found, a significant difference between spring and autumn wing lengths, which is consistent with previous results (Pásztory-Kovács 2013). Birds captured in autumn had longer average wing length than in spring, but the difference falls within the potential growth due to moult (0.4–0.8 mm). Males had longer wings than females both in spring and autumn. The migration strategy of the Pied Flycatcher, as well as of its relative, the Spotted Flycatcher (Török 2009*a*) differs significantly between sexes. In spring, males migrate faster than females, crossing instead of avoiding ecological barriers, performing a loop migration (Newton 2008). Harnos *et al.* (2015*a*,*b*) based on the different wing length, sex ratios in the two seasons, and the timing of spring arrival, came to similar conclusions. They found that Pied Flycatchers show sex dependent migration patterns with increasing protandry in spring – males return earlier from the wintering areas than females. In our study the differences in the average wing length of this species between spring and autumn also indicate the existence of loop migration, but do not prove it clearly because the difference is smaller than the expected growth due to moult.

The Wood Warbler has an extremely large distribution range (Cramp & Brooks 1992), and it still expands northwards in Scandinavia (BirdLife International 2004). Birds nesting in Europe and Siberia reach Africa through the Central and Eastern Mediterranean, while birds originating from Western Europe pass through the Italian Peninsula (Cramp & Brooks 1992). It is evident from recapture data that birds nesting on the British Isles perform a clockwise loop migration (Wernham *et al.* 2002). Since the average wing length of captured birds during the autumn migration period was much shorter than the average wing length of birds nesting in the north (Finland), it can be assumed that most of the birds do not migrate through Hungary in this season (Miklay & Csörgő 1991). The significantly longer average wing length in spring may originate from northern birds passing through the Carpathian Basin. This assumption is consistent with the existence of counter-clockwise loop migration. Based on Hungarian (Ócsa) ringing data, we know that the average wing length of adult birds captured in spring and in autumn is different, and longer winged birds appear earlier in this area in both seasons (Gyurácz & Csörgő 2009*b*). The large differences in our study in the average wing length between

seasons also confirm our suggestion that the Wood Warbler is a loop migrant in the Carpathian Basin.

The Spotted Flycatcher winters south of the Sahara. Populations breeding in Europe have two main migration routes. Birds originating from Scandinavia migrate through Great Britain and the Iberian Peninsula towards Africa. Birds nesting east of the 12° E parallel migrate in a south/south-southeasterly direction (Cramp *et al.* 1993). In Hungary, we have recaptures from Sweden and Lithuania (Török 2009*a*), suggesting that birds belonging to the Eastern Scandinavian population migrate through the Carpathian Basin. Among the Spotted Flycatchers ringed in Hungary, there was only one bird recaptured in Tunisia during the spring migration period, indicating a southwesterly return direction. We suggest that the return journey is shorter and more directly targets the nesting areas (Török 2009*a*), resulting in a loop migration. British data confirm this (Wernham *et al.* 2002, Bønløkke *et al.* 2006) and earlier studies also mention the possibility of this migration pattern (Pearson 1990, Pearson & Lack 1992). Since birds from the north have longer wings, the difference found in our study – significantly longer average wing length in spring than in autumn – was probably due to northern-breeding trans-migrant birds. The difference was not only significant, but it also exceeded the growth interval of moult. Based on these facts, we suggest that Spotted Flycatchers are loop migrants in this region.

The Red-backed Shrike is a typical counter-clockwise loop migrant (Zink 1975, Berthold 2001, Newton 2008, Fuisz & Csörgő 2009, Tøttrup *et al.* 2012). The main autumn route lies west of the 33° E, while the spring route east of Lake Victoria (Cramp *et al.* 1993). Surprisingly, in our study, we have not found seasonal difference in Red-backed Shrike wing lenghts. We suggest that loop migration can not be detected using morphological data in this species, at least not in the Carpathian Basin, because the spring and autumn routes lie too close to each other at this latitude. The maximum extent of the loop is in the Eastern Mediterranean region. Research with light-level geolocators confirms this fact: the widest part of the loop is between the Italian Peninsula and the Middle East. On the other parts of the migration route, the loop cannot be detected (Tøttrup *et al.* 2012).

Adult individuals of the Willow Warbler perform complete postnuptial and prenuptial moult (Svensson 1992) a rare moult strategy in European passerines. Birds migrating through the Carpathian Basin may arrive from the Baltic region, the Scandinavian Peninsula and Western Russia (Gyurácz & Csörgő 2009*c*). In our study the Willow Warblers' average wing length in autumn was much shorter than spring despite the moult after the breeding season. In Hungary there are only a few recoveries of birds originating from the north (longer wing), and birds captured in autumn have on average shorter wings than birds nesting on the Scandinavian Peninsula. So the greatest part

of birds captured in autumn probably originates from the Hungarian or from a neighbouring population (Miklay & Csörgő 1991). This species does not show sexual colour dimorphism, but males have longer wings than females, (Tiainen 1982, Tiainen & Hanski 1985, Ellrich *et al.* 2010). However, sex determination is possible only during the breeding season (Norman 1983). Due to lack of reliable data on male vs. female wing lengths, we cannot exclude that the significant differences in the average wing length originated from the differences between sexes. According to another explanation in autumn the birds from the north do not migrate through Hungary and the Carpathian Basin Gyurácz & Csörgő (2009*c*) claimed that in autumn northern Willow Warblers do not migrate through the Carpathian Basin, but do so in spring, so they are loop migrants. Other studies confirm this assumption: Willow Warblers perform a counter-clockwise loop migration in Africa. Birds from Europe pass through Uganda to the wintering sites in autumn, but they use a more easterly route, along coastal regions in the spring (Pearson 1990, Pearson & Lack 1992).

Among species performing postnuptial moult, the Common Nightingale, the Savi's Warbler and probably the Pied Flycatcher; among species performing prenuptial moult, the Wood Warbler and the Spotted Flycatcher proved to be a loop migrant in the Carpathian Basin, and the single species performing double moult, the Willow Warbler probably follows this migration pattern as well. Recapture data of the Wood Warbler and the Pied Flycatcher also confirm that these species are loop migrants. For the Common Nightingale, the Savi's Warbler and the Willow Warbler, the loop migration strategy was not known before.

Differences between spring and autumn wing lengths can be adequate to detect loop migration, but the moult strategies (the degree of the wing length growth from the moult), the breeding sites and distribution ranges of the different populations need to be known. In species showing sexual dimorphism, it is worth to make sex-specific comparisons, because the migration strategies of the two sexes may significantly differ.

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